

Transient coordinated activity within the developing brain's default network

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Abstract The concept of a brain default network postulates that specific brain regions are more active when a person is engaged in introspective mental activity. Transient functional coordination between groups of neurons is thought to be necessary for information processing. Since children develop introspection as they mature, regions of the default network may establish increasing functional coordination with age, resulting in fewer fluctuations in synchronization patterns. We investigated the transient coordinated activity in regions of the default network in seventeen children aged 11 months to 17 years of age using EEG recordings while subjects were resting quietly with eyes closed. The temporal and spatial fluctuations in the phase synchrony patterns were estimated across sites associated with the default network pattern and compared

to other regions. Lower variability of the spatio-temporal patterns of phase synchronization associated with the default network was observed in the older group as compared to the younger group. This indicates that functional coordination increases among regions of the default network as children develop.

Keywords Default network · Instantaneous phase · Synchronization · Fluctuations · Electroencephalography

Introduction

The electroencephalogram (EEG) has emerged as a tool to evaluate normal brain dynamics in adults and children (Fell et al. 2003; Cantero and Atienza 2005; Bastiaansen and Hagoort 2006; Serrien 2008). Specifically, measures derived from the phase synchrony of EEG signals have been used to estimate the transient coordinated activity that is characteristic of brain dynamics in cognition. Transient coordinated activity reflects the temporal recruitment (temporal dynamics) of groups of neurons from different brain regions (spatial dynamics) into functionally connected networks. Evaluating coordinated EEG activity patterns in children of different ages could thus be important to understand the profound changes in brain processes that give rise to cognitive functions as children develop. Synchronized brain activity has been documented in a myriad of studies (Perez Velazquez and Wennberg 2009), and particularly its relation to cognition is currently being studied under a wide variety of scenarios. Coordination among neuronal groups into transient networks is believed to be necessary for information processing in normally functioning brains (Tononi et al. 1994; Bressler and Kelso 2001; Ghosh et al. 2008b). Different groups of

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neurons are transiently recruited and functionally connected into networks at the millisecond time scale to allow for task performance or other forms of mental activity. However, rather than the magnitude of the synchrony that is often specified as some synchronization index (Mormann et al. 2000), it is the fluctuations in synchronization that probably best reflects healthy information processing and thus confers adaptability on the individual. Periods of coordinated activity that are over-extended in time or space tend to be associated with diseases (Perez Velazquez et al. 2007). In our study, we assessed fluctuations in brain coordinated activity within a spatially predefined network, across two age groups, endeavoring to characterize developmental change in the coordination dynamics revealed by entropy and spatial complexity measures derived from the phase synchronization found in electrophysiological recordings.

One kind of mental activity that stands in contrast to task performance is the introspection or reflection that takes place when task demands are low or task performance is completed. This sort of mental activity is thought to be the product of activation within the brain's default network (Mantini et al. 2007; Raichle and Snyder 2007; Buckner et al. 2008; Fair et al. 2008; Laufs 2008; Greicius et al. 2009). After the pioneering work of Ingvar in the 1970s showing “hyperfrontal” activity when the brain is at rest (Ingvar 1974), several investigations have revealed that some brain regions are preferentially activated when the brain is in the at-rest state, that is, when individuals are not focused on the external surroundings. The activity in these regions decreases during task performance. These regions have been thus hypothesized as comprising the default network (Raichle et al. 2001; Chen et al. 2008; Greicius et al. 2009), and include the posterior cingulate, medial prefrontal cortex, bilateral parietal cortices, bilateral temporal cortices and bilateral parahippocampal gyri (van de Ven et al. 2004; Buckner et al. 2008; Fair et al. 2008). Activity within the default network has been previously characterized as “noise” resulting from stochastic neuronal firing. However, recent studies using neuroanatomical measures of connectivity in the primate brain have shown that the background brain activity is not random oscillations but is instead related to non-task-oriented thought and the development of integrated synapses (Ghosh et al. 2008a, b). As a child develops the ability for introspection, daydreaming and future planning, the regions involved in the default network are hypothesized to emerge as an interconnected system.

To estimate connectivity, most studies to date have used functional magnetic resonance imaging (fMRI), which allows fine-grained visualization of multiple brain regions and especially medial structures (Mantini et al. 2007; Buckner et al. 2008; Fair et al. 2008; Gao et al. 2009).

EEG, on the other hand, does not provide fine-grained spatial information on brain structures, but its temporal resolution is particularly well suited to assess the dynamics of neuronal connectivity. In addition, EEG records multiple frequencies simultaneously. The occipital alpha frequency that develops as children mature has been considered the global background rhythm (Kelway 2003), but Nunez (2000), Buzsaki (2006), and others propose that there are multiple global frequencies that result from dynamic interactions between local neuronal networks and global brain systems. Many studies have used phase synchrony for investigating fluctuations in transient connectivity (Friston 2001; Varela et al. 2001; Lutz et al. 2002; Chen et al. 2008). Since, in this manner, most cortical regions can be evaluated simultaneously, a variety of EEG patterns may be observed in the brain's “resting state” (Laufs et al. 2003). A recent study simultaneously evaluated EEG phase synchrony and fMRI in normal adults, identifying several resting state constellations that tap the default network (Jann et al. 2009). Consistent with this approach, our study was designed to evaluate the development of transient functional connectivity among regions of the brain's default network in normally developing children, utilizing entropy and spatial complexity that are derived from measures of phase synchronization (Pikovsky et al. 2001). We hypothesized that entropy and spatial complexity among sites tapping the default network would be lower in older children than younger children, demonstrating a developmental increase in functional coordination within the default network.

One clarification that deserves to be noted here is the use of the term “network” in our study. Our chosen EEG sensors, as detailed in “Methods”, correspond to the cortical default network areas identified in neuroimaging studies. However, we are not thinking in terms of a functionally interconnected network in the sense of one cortical region under one EEG sensor directly interacting with another region under another sensor, but rather our intention was to assess the variability of synaptic arrivals (this is because we use scalp EEG and it is the summation of synaptic potentials that make up most of the signal) at some cortical areas that correspond to the neuroimaging default areas, and to compare the variability in these regions to that found in other regions, as perhaps an illustration of the synaptic re-arrangements due to pruning that may result in the fixing or establishment of the synaptic inputs during development. Our study was designed to evaluate the development of the variability in the synchrony of incoming activity in terms of the spatio-temporal fluctuations of phase differences derived from the EEG recordings, specifically in areas of the brain's default network versus other areas. Measures of the spatio-temporal fluctuations that we used were the entropy of the phase

differences, the rate of fluctuations of the phase differences and the spatial complexity of the phase synchronization. Considering that the developing brain undergoes a process of synaptic pruning and other maturation mechanisms, our main hypothesis is that there will be less variability in older children compared with a younger age group.

Methods

Demographics and EEG recordings

A convenience sample of 17 normal children, aged 11 months to 17 years, was recruited to participate in the study. Inclusion criteria consisted of minimal head circumference required for a 19 channel EEG montage, parental consent and participant assent where applicable. Participants were excluded if they had a history of seizure disorder, head injury or psychiatric disorder. Parental interviews utilizing the Pediatric Cerebral performance Category score (PCPC) validated the children's normal function for their age. Each child had a 30 min EEG recording, using the international 10–20 montage. The subjects were instructed to keep their eyes closed and not to talk or focus on anything in particular. The youngest children, who could not cooperate with the instructions, were monitored for episodes of rest, with eyes closed. The EEGs were monitored to ensure that the children did not fall asleep. The EEGs were recorded using a sampling rate of 500 Hz and a band pass filter of 1–70 Hz, with a 60 Hz notch. All EEGs were read by electroencephalographers and confirmed to be normal EEG recordings for each child's age. Four non-overlapping epochs of 10 s were extracted from each recording. The four segments were selected from periods of quiet wakefulness with eyes closed and were free of muscle or movement artifact.

The choice of EEG electrodes to represent the default network was based on fMRI studies done in adults and children (Mason et al. 2007; Fair et al. 2008; Gao et al. 2009). The areas of interest for the default region were the fronto-polar region (sites FP1 and FP2), temporal lobes (T3 and T4), inferior temporal lobes (T5 and T6) and parietal lobes (P3 and P4). The non-default region consisted of the remaining 11 channels: bilateral frontal (F3, F7, F4, F8), bilateral central (C3 and C4) and bilateral occipital lobes (O1 and O2). The locations of these EEG sensors are depicted in Fig. 1.

Hilbert transform

Each of the EEG epochs was first processed using a Laplacian transform to 1. avoid the potential confounding effects of the reference electrode on synchronization

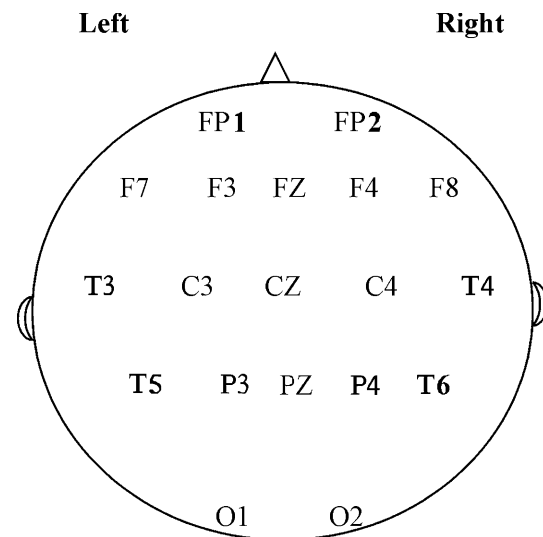


Fig. 1 Placement of the EEG electrodes in the 10/20 montage. Those electrodes corresponding to regions identified with default area are highlighted in *bold*

(Guevara et al. 2005) since this transformation mathematically approximates a reference-free signal (Nunez et al. 1997; Hagemann et al. 2001) and 2. To remove volume conduction effects (Nunez et al. 1997; Winter et al. 2007). Next, signals were filtered to within five pre-selected frequency bands (4, 8, 14, 25 and 35 Hz), using a Constrained Least Squares Finite Impulse Response filter (FIRCLS) with a pass-band of ± 2 Hz around each selected frequency. To estimate the variability of the phase differences between EEG sensors, the instantaneous phases for each EEG signal at the individual pre-selected frequencies were obtained using the Hilbert transform. The Hilbert transform is particularly useful for analyzing waveforms that are non-stationary and noisy (Pikovsky et al. 2001).

Entropy and rate of phase fluctuations

The EEG channels were divided into the 2 groups: default (FP1/FP2, T3/T4, T5/T6 and P3/P4) and non default (F7/F8, F3/F4, C3/C4, O1/O2, Fz, Cz, Pz) regions. The phase differences between two EEG channels were divided in 20 bins (see Fig. 2) and the entropy associated to this distribution was calculated according to the standard equation

$$S = - \sum_{i=1}^{20} p_i \times \ln(p_i)$$

where p_i are the probabilities computed for each phase difference. This calculation was performed for all possible pair combinations in each of the two groups at each of the five frequency bands. The average of all possible pair phase differences within each group, at each frequency produced one value, “entropy” and was then used for the statistical analysis.

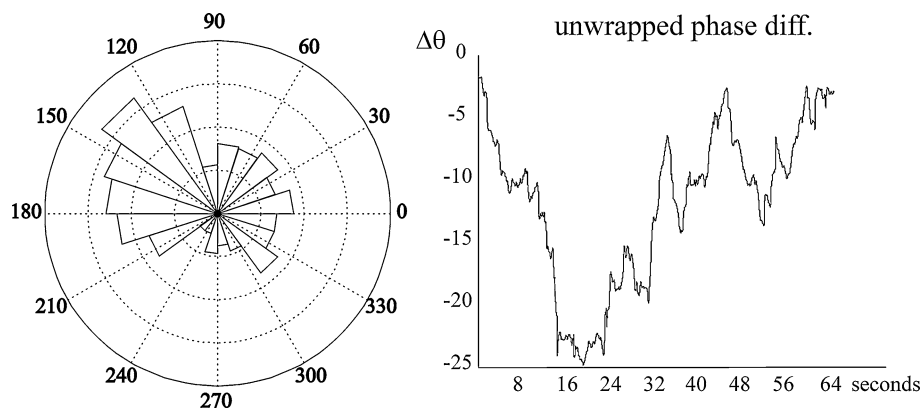


Fig. 2 The angles corresponding to the phase differences between two EEG signals (T3 and T4 in this example), were divided in 20 bins and used to estimate the probability of the occurrence of each angle. The entropy was then computed as described in the text. The right-

hand side of the *graph* is the time series of the unwrapped phase difference between two EEG signals that is used to assess the rate of fluctuations in phase difference

The fluctuations in the phase difference time series were estimated as the absolute value of the derivative of the time series: $|d(\Delta\theta)/dt|$ where $\Delta\theta$ is the phase difference between two selected signals (Fig. 2, right hand side graph, shows one example of a typical time series of phase differences). In this manner, both small fluctuations and large ones (phase slips) are captured. As above, this calculation was performed for all possible pair combinations in each of the two groups (default and non default) at each of the five frequency bands. The resultant average of the fluctuations in the phase differences of all possible pairs at each frequency was then used for the statistical analysis.

Spatial complexity of EEG phase synchrony

The spatial complexity of the phase synchronization pattern was calculated as described in Garcia Dominguez et al. (2008), which measures how predictable the synchrony indices (mean phase coherence) are for each channel using the spatial information from the neighboring values.



Fig. 3 An example of the head plots of the synchrony indices evaluated at 14 Hz of 2 subjects at rest with eyes closed. The head plot of the 11-month-old boy is on the left and that of the 10-year-old boy is on the right. The range of synchrony values are colour coded, where dark red indicates maximal synchrony (+3) and dark blue indicates no synchrony (−2)

Smooth (homogeneous) spatial patterns of synchrony indices make them very predictable and are considered indicators of low complexity and will have a lower value. In contrast, a high degree of spatial variability (heterogeneity) with unexpected fluctuations between neighbouring sites represents high spatial complexity and will have a higher value. Figure 3 depicts two examples of the spatial distribution of the synchrony index (using a surrogate correction) on which the spatial complexity estimation is based. The spatial complexity is affected by both spatial and dynamical properties, for example it is expected to increase with the number of active sources. Briefly, the “mean phase coherence” (Mormann et al. 2000) is first computed from the instantaneous phase differences for each of the 171 pair of channels (derived from 19 EEG channels). Each particular channel has a synchronization index with each of the remaining 19-1 channels, these values can be mapped as surface over a 2-dimensional representation of the channel position. Since there are 19 of such maps each one can be identified as M_j ($j = 1, \dots, 19$). On each map M_j we compute a spatial complexity index and assign it to the respective j channel. Large values of this spatial complexity index correspond to visually complex patterns in M_j , in which specific synchrony index cannot be easily predicted from those of its neighbors. Figure 3 illustrates two of these M_j maps one from a 11-month-old boy and one from 10-year-old boy. After calculating the spatial complexity of the EEG phase synchrony for each of the 19 channels, the channels were then divided into the two groups: regions associated with the default network and the non-default network for comparison and statistical analysis.

Statistical analysis

ANOVA was first used to evaluate the 4 separate time epochs extracted from the raw recording and test the null

hypothesis that these different samples were statistically the same, representing the same quiet resting state with eyes closed. The four epochs were then averaged for each participant and this average was used to compute the spatial complexity. ANOVA was again used to compare the mean spatial complexity of EEG phase synchrony between 4 groups: older children default network, older children non-default network, younger children default network and younger children non-default network at each of the frequency bandwidths in a $2 \times 2 \times 5$ ANOVA. The same approach was used to evaluate the differences in both entropy and rate of phase fluctuations.

Results

Entropy of the distribution of phase differences within the default network

The entropy of the identified default channels depicted in Fig. 1 (FP1/FP2, T3/T4, T5/T6 and P3/P4) for all 17 children, was computed from the phase differences at the selected frequencies of 4, 8, 14, 25 and 35 Hz as described in the “Methods” section. These values are shown in Fig. 4. It was noted that the entropy values of children older than 5 had a wider range, particularly for the default channels (panel A). Hence, based on this observation, the 17 subjects were divided into 2 groups: “young” ≤ 5 years, ($n = 8$, mean age 2.6 years, range 0.9–5 years) and “old” > 5 years, ($n = 9$, mean age 10.2 years, range 6–17 years).

When the entropy values associated with the default and non-default channels between the “old” and “young” groups were compared, the differences were significant as shown in Table 1. The young group had greater entropy values. In addition, as also shown in the table, the comparison of the two cortical areas (default and non-default) within each group resulted in a significant difference only in the case of the older group: note that the entropy was larger for the non-default EEG channels, suggesting that the older the child, the more “organized” the coordinated activity is in the default areas. The “young” group had similarly high entropy values for the phase differences in both cortical areas, suggesting that at this early age the coordinated activity is similar throughout the cortex.

Rate of fluctuations in phase difference

The rate of fluctuations in the phase difference was derived as detailed in “Methods”, and basically indicates rate of phase slips found in the phase difference time series. Figure 2 shows a typical temporal evolution of the unwrapped phase difference. Table 2 shows the comparison between the values associated with the default and

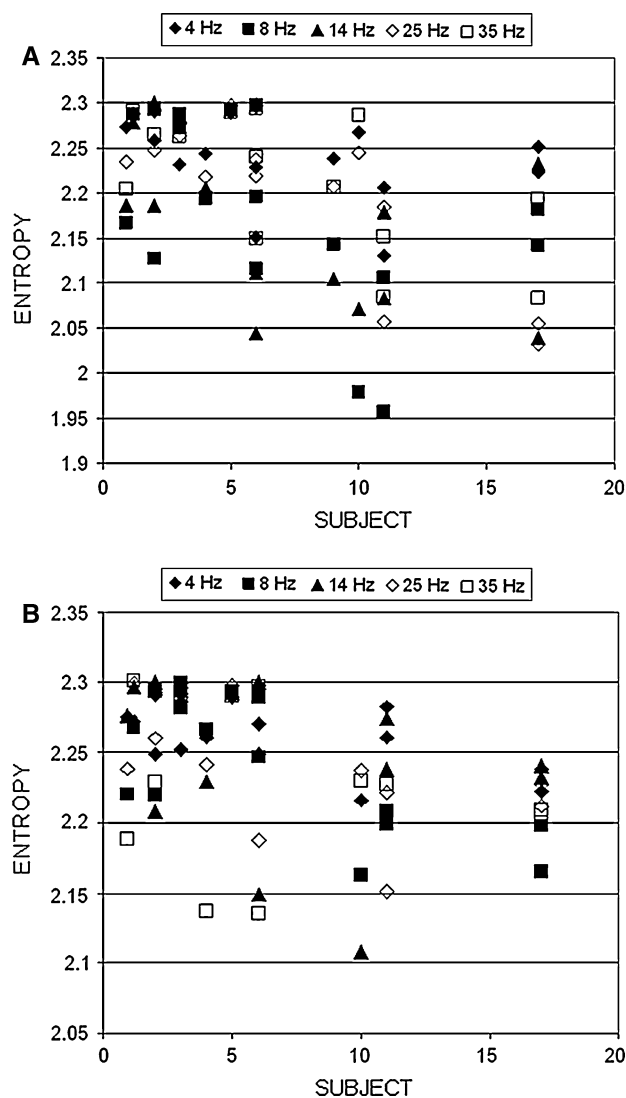


Fig. 4 Entropy values of the distribution of phase differences for all subjects for the regions of the default areas (a) and for the other regions of the brain (b). Each geometric symbol represents the entropy value at one of the five frequencies for each subject

non-default channels for the old and young group, and within each group. The values were significantly different between the groups, but not within groups. Lower fluctuation rates were seen in the older group that correlated with the lower entropy values presented above in Table 1, further suggesting that the coordination dynamics becomes more organized temporally and spatially as development progresses.

Spatial complexity

The mean spatial complexity values of phase synchrony, computed from the spatial distribution of the synchrony index (as shown in one example in Fig. 3) are presented in Table 3 along with the ANOVA of the 4 groups at each of the selected frequencies. Additionally a Bonferroni

Table 1 The ANOVA results of the overall effect of age on entropy; the effect of the default network on entropy in the different age groups and lastly the effect of frequency on entropy with respect to both the networks and age

| Source term | Degrees of freedom | Sum of squares | Mean square | F ratio | Prob level power ($\alpha = 0.05$) |
|-------------------------|--------------------|----------------|-------------|---------|--------------------------------------|
| Age | 1 | 0.051 | 0.051 | 10.54 | 0.0014 |
| Default (age) | 3 | 0.027 | 0.091 | 25.71 | <0.0001 |
| Frequency (age default) | 19 | 0.46 | 0.024 | 8.84 | <0.0001 |

The Bonferroni correction demonstrated that the “young default” (mean entropy = 2.257 ± 0.002) and the “old default” (mean = 2.166 ± 0.008) groups were significantly different from each other, as were the “young non default” (mean = 2.269 ± 0.0014) and “old non default” (mean = 2.22 ± 0.002) groups. In addition the mean overall entropy difference between the “young non default” (mean = 2.26 ± 0.002) and “old default” (mean = 2.19 ± 0.007) were statistically significantly different, with the young group having the higher entropy. With respect to frequency, 8 and 35 Hz were statistically significantly different between the young and old default groups, with the “old default” group again having lower entropy values

Table 2 The ANOVA results of the overall effect of age on the rate of fluctuations; the effect of the default network on the rate of fluctuations in the different age groups and lastly the effect of frequency on the rate of fluctuations with respect to both the networks and age

| Source term | Degrees of freedom | Sum of squares | Mean square | F ratio | Prob level power ($\alpha = 0.05$) |
|-------------------------|--------------------|----------------|-------------|---------|--------------------------------------|
| Age | 1 | 0.00032 | 0.00032 | 24.08 | <0.0001 |
| Default (age) | 3 | 0.00034 | 0.00011 | 8.47 | <0.0001 |
| Frequency (age default) | 19 | 0.0011 | 0.00006 | 5.84 | <0.001 |

The Bonferroni correction demonstrated that the “young default” (mean rate of fluctuations = 0.018 ± 0.004) and the “old default” (mean = 0.014 ± 0.002) groups were significantly different from each other, as were the “young non default” (mean = 0.017 ± 0.004) and “old non default” (mean = 0.015 ± 0.002) groups. In addition the mean rate of fluctuations difference between the young non default and old default were statistically significantly different. With respect to age, the “young” group had a higher rate of fluctuation (mean = 0.17 ± 0.004) than the “old” group (mean = 0.14 ± 0.002). With respect to frequency, 4 Hz was statistically significantly different, with the “old default” group having the lower rate of fluctuations (mean 0.0096 ± 0.0009) compared with the “young default” (mean 0.013 ± 0.006)

Table 3 The ANOVA results of the overall effect of age on the mean spatial complexity; the effect of the default network on mean spatial complexity in the different age groups and lastly the effect of frequency on the mean spatial complexity with respect to both the networks and age

| Source term | Degrees of freedom | Sum of squares | Mean square | F ratio | Prob level power ($\alpha = 0.05$) |
|---------------------------------|--------------------|----------------|-------------|---------|--------------------------------------|
| Age | 1 | 0.016 | 0.016 | 16.51 | <0.0001 |
| Default network (age) | 3 | 0.018 | 0.0063 | 6.36 | 0.0004 |
| Frequency (age default network) | 19 | 0.034 | 0.0018 | 1.84 | 0.02 |

The Bonferroni correction demonstrated that the mean spatial complexity of the EEG phase synchrony in the “young default” group (mean = 0.18 ± 0.02) and the “old default” group (mean = 0.16 ± 0.02) groups were significantly different from each other, as were the “young non default” (mean = 0.19 ± 0.03) and “old non default” (mean = 0.17 ± 0.02) groups. With respect to the overall age difference, the “young default” (mean = 0.18 ± 0.02) had a higher mean spatial complexity than the “old default” group (mean = 0.16 ± 0.02). With respect to frequency, the mean spatial complexity at 4 Hz was statistically different (highest with respect to the other frequencies) within each of the 4 groups, but again lower in the older age group: “young default” group (mean = 0.19 ± 0.02); “old default” group (mean = 0.18 ± 0.02); “young non default” (mean = 0.2 ± 0.02) and “old non default” (mean = 0.18 ± 0.02)

adjustment of the ANOVA results demonstrated significant differences between age groups and between the default and non-default regions. Within each of the 2 age groups the default regions’ spatial complexity means were lower than the non default regions. However, comparing the default regions *between* the 2 age groups, showed that the older group had a lower spatial complexity in the default region.

Within the region of the default network, at all selected frequencies, the bilateral parietal cortices (EEG sensors

P3 and P4) had a statistically significant difference in spatial complexity ($p < 0.001$), with the younger age group having the higher value (see Fig. 5 for an example).

Discussion

The main observation in this study was the lower variability of the spatio-temporal patterns of phase synchronization associated with the default region in the older group

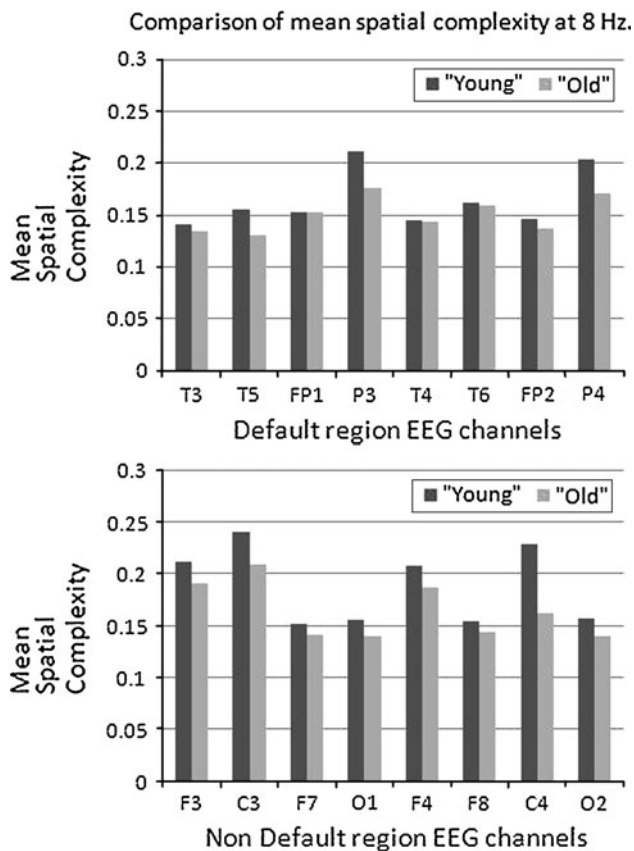


Fig. 5 A comparison of the spatial complexity of the EEG synchrony pattern in the default areas (*top graph*) and the non-default areas (*bottom graph*) between the young group (*black*) and the older group (*gray*) at 8 Hz

as compared to the younger group. In other words, the default areas seem to receive a less variable (hence more synchronous) input as compared with non-default regions in older children, while in young children both areas seem to present a similar degree of high variability, as compared with the older group. This conclusion is based on the decreased entropy and rate of phase fluctuations among regions associated with the default region in the older group as compared to the younger group as well as in the lower spatial complexity of the EEG phase synchrony in the regions associated with the default network in the older group. These findings support our hypothesis that both the temporal and spatial dynamics would decrease in the region of the default network in older children compared with younger. In addition, as we see overall, a decrease in entropy and spatial complexity also occurs in the non default regions in the older group, indicating that the more mature brain networks may become entrained in longer periods of synchronization compared to the younger brain.

A potential complication of this study is associated with scalp EEG signals that are known to be prone to volume conduction phenomena. Due to this spread of currents on

the scalp, the EEG sensors record not only activity directly below them, but also from neighbouring areas. However, in addition to the use of the Laplacian transform, which has been known to remove volume conduction effects for EEG coherence (Nunez et al. 1997; Winter et al. 2007), we also partitioned the set of EEG electrodes into two groups. If volume conduction were to be a problem, then the net effect of volume conduction would be to render all comparisons not significant. This can be visualized by considering, for example, one electrode in the default region (left temporal, T3) that records activity from that cortical area along with activity from a neighbouring non-default-region (left central, C3). But, at the same time, the neighbouring sensor that is on top of the non-default area (C3) would also record activity from the adjacent default area (T3). This would have been a problem if we had not evaluated the variability in the non-default electrodes, because then we would not know whether the “default” sensors were recordings strong sources located in the neighbouring non-default areas. The fact that group differences between default and non-default signals were observed, recorded at adjacent sensors, suggest a good degree of specificity in the association between regions of cortex and recording sites. A second observation that works against the likelihood of serious distortions due to volume conduction is that *more* variability was observed in younger children than older children. With age, skull thickness is known to decrease while cortical volume increases. Both sets of changes would increase the specificity with which surface electrodes tap discrete cortical regions. Thus, less (not more) variability, due to greater spatial overlap would be expected in younger children, if volume conduction were an important contributor to observed scalp results.

Our study was focused on the comparison between EEG sensors that would detect activity in the default versus non-default cortical areas, but not on the global state of the whole cortex. However, our findings of higher variability in younger brains could be a more general characteristic that applies to other cortical areas, before the pruning of spurious synaptic connections has begun. Thus, it could be argued that our findings simply reflect the larger numbers of synaptic contacts in younger children (Fair et al. 2007).

Normal brain development is a dynamic process that involves myelination, synaptogenesis, synaptic pruning, (denoted by the thinning of gray matter in the cortex), and consolidation of long-range connections into functional networks (Gogtay et al. 2004; Sowell et al. 2004; Lewis 2005; Fair et al. 2008; Kaiser 2008). The brain, as a self-organizing system, will develop the global systems and subsystems required to process information and engage in tasks required to sustain learning and navigate the social and nonsocial worlds. The final “product,” the mature brain, will be an efficient system reflecting the functional

combinations of synaptic connectivity for that individual (Cherniak et al. 2004). As a child develops the ability for introspection, daydreaming and future planning, the regions involved in the default network are hypothesized to emerge as an interconnected system. Earlier work postulated the dynamic interrelationship between segregated brain regions that are fixed anatomically and then functionally integrated into networks to accomplish tasks or process information through coordinated activity (Tononi et al. 1994; Sporns 2003). Recent theoretical work has indicated that, as myelination proceeds, the brain stabilizes a global network state (Qubbaj and Jirsa 2009). Considering all these observations, the higher variability we observed in the younger group could reflect the fact that, at those developmental stages, there is an overabundance of connections that will be pruned later on, leading to many pathways of connectivity that, through their alternation, give rise to more fluctuations in synchrony and its derivatives.

Thatcher et al. (2007), in a study of 458 children, used EEG coherence and phase differences to explore the developing brain and found that there were large increases in EEG coherence in older children compared with younger children. There are few other studies to which to compare our results, as most of the work on the default network has been in adults. However, our findings are consistent with two paediatric studies using fMRI (Fair et al. 2008; Gao et al. 2009). Fair et al. compared the default network in 7- to 9-year-olds with that in adults, and found that this network was more sparsely connected in the children. These findings mirror our observation of decreased entropy and spatial complexity for the older age group. This may reflect the increased connectivity and efficiency in the “older” brains. Gao et al. (2009) studied children aged 2 weeks to 2 years and found an increasing number of regions associated with the default network in the older children, with an emphasis on the region of the posterior cingulate gyrus. While Gogtay et al. (2004) did not examine the default network specifically; their longitudinal pediatric MRI study showed that the maturational process is characterized by gray matter loss that begins in the dorsal parietal cortices. This is consistent with our finding of the greatest age difference in spatial complexity in the parietal region. Another recent study reported increased variability in brain signals with age (McIntosh et al. 2008); however these were associated with the performance of memory tasks, not resting states. Perhaps, then, older brains demonstrate more variability associated with the integration and segregation of information needed to perform behavioural/cognitive tasks, consistent with the long-range network activity reported by Fair et al. (2008).

To conclude, our results indicate that both the temporal dynamics (entropy and rate of phase fluctuations) and spatial dynamics (spatial complexity) become less variable

in regions associated with the default areas in older as opposed to younger children. These findings suggest greater functional connectivity in a hypothesized network with age, consistent with previous neuroimaging results from fMRI studies, and they support the proposition that the default network becomes “wired” with age as children develop the capacity for introspection. While these results are preliminary, they support the use of EEG as a tool for investigating the development of brain dynamics in children.

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